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Mechanisms of Interactions Among *Sphagnum* Species Along Water-Level Gradients

by

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With 7 Figures

Abstract: This review deals with the biology of hummock- and hollow-inhabiting *Sphagnum* species, concentrating on the mechanisms behind interspecific competition and coexistence in bogs and poor fens. Even though different species are involved in oceanic and continental climates it is suggested that the mechanisms are similar even between remote areas. Hollow species have a potential for a higher growth rate than hummock species, and all species show increasing photosynthesis and growth in hollows than at positions above the water table. There seems to be no general difference between hummock and hollow species in their ability to perform photosynthesis at low water content or in their ability to recover from desiccation, but hollow species are more often dry than hummock species. The upper limit of the species is related to water transport ability. Hollow species can grow high up on the hummock if their shoots are provided with water through lateral transport from the surrounding matrix of hummock species. Transplant experiments have shown that patches of the hummock species *S. fuscum* decreased in cover initially in the hollows but recovered and showed a highly variable result after a decade. It was not outcompeted by the hollow species. The experiments also suggest that only small differences exist in competitive ability among hollow species and that competitive ability may vary from season to season and between years. The outcome of competition can be variable even within narrow height ranges. The ability of *Sphagnum* to regenerate sexually and asexually is discussed, and the need for further research on phenotypic plasticity, shoot demography, and population genetics is stressed. It is important that such research integrates field and laboratory studies.

Zusammenfassung: Diese Besprechung behandelt die Biologie von bülten- und schlenkenbewohnenden *Sphagnum*-Arten unter Berücksichtigung der Mechanismen interspezifischer Konkurrenz und Koexistenz in Hochmooren und nährstoffarmen Flachmooren. Auch wenn in ozeanischen und kontinentalen Gebieten verschiedene Arten

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vorkommen, so wird doch vermutet, daß die Prozesse auch in weit voneinander gelegenen Gebieten vergleichbar ablaufen. Schlenkenarten haben ein Potential für größere Zuwachsraten als Bültenarten. Alle Arten zeigen zunehmende Photosynthese und Wachstum in Schlenken, aber nicht oberhalb der Wasserstandslinie. Bülten- und Schlenkenarten scheinen gleichermaßen fähig zu sein, bei niederem Wassergehalt assimilieren oder Trockenperioden überdauern zu können, doch sind Bültenarten häufiger trockenen Bedingungen ausgesetzt. Die obere Grenze einer Art wird durch die Wassertransportfähigkeit gesetzt. Schlenkenarten können weit auf die Bülten vordringen, wenn ihre Sprosse genügend mit Wasser durch lateralen Transport aus der die Bültenarten umgebenden Matrix versorgt wird. Verpflanzungsexperimente haben gezeigt, daß die Deckung der Bültenart *Sphagnum fuscum* in Schlenken zwar ursprünglich abnahm, sich aber erholte und nach zehn Jahren variable Resultate aufwies und nicht von Schlenkenarten verdrängt wurde. Aus diesen Versuchen ergibt sich auch, daß wohl nur geringe Unterschiede in der Konkurrenzkraft unter Schlenkenarten bestehen, welche innerhalb der Jahreszeiten wie auch von Jahr zu Jahr schwanken kann. Konkurrenzschwankungen können sogar innerhalb verschiedener Längenabschnitte des *Sphagnum*-Polsters festgestellt werden. Die Fähigkeit sexueller und asexueller Regeneration bei *Sphagnum* wird besprochen und die Notwendigkeit weiterer Untersuchungen über phänotypische Plastizität, Sproßdemographie und Populationsgenetik unterstrichen. Es ist wichtig, daß hierbei sowohl Feld- wie Laborbetrachtungen einbezogen werden.

Keywords: competition, growth, habitat, morphology, niche, physiology, *Sphagnum*, transplant experiments, water level.

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Introduction

Although *Sphagnum* mosses occur in a wide range of habitats, most studies of their ecology have been made in the boreal peatlands they inhabit and dominate. These are bogs (ombrotrophic mires) and poor fens (minerotrophic, but acidic and with low calcium concentration). The surface patterns so characteristic of these mires have fascinated plant ecologists since the turn of the century. The idea of cyclic succession between hummock and hollow stages (von Post & Sernander 1910) was influential, and for half a century the mire literature was full of examples in which successional schemes were drawn on the basis of observed patterns. Osvald's study (1923) of Komosse is the most well-known case, and it inspired a large number of studies in Sweden and elsewhere, suggesting that interspecific relations between the *Sphagnum* species that created the patterns could be interpreted in successional terms.

It is now generally agreed that there is little evidence supporting the cyclic regeneration theory, and it also remains an enigma on what evidence the theory was initially constructed (Backéus 1972, 1991; Barber 1981). Surprisingly, it survives in rather recent textbooks (e.g., Harper 1977).

In recent decades much knowledge has accumulated about the growth, production, and physiological ecology of *Sphagnum*. The literature up to 1984 is covered by the reviews of Clymo and Hayward (1982) and Andrus (1986). In this paper I will summarize the information that forms the basis of current understanding of interspecific relations among *Sphagna*, concentrating on the mechanisms behind competition in bogs and poor fens. It is a convenient fact that, although studies of *Sphagnum* ecology have been made as far apart as Russia, Finland, Sweden, Norway, Great Britain, USA, and Canada, the data are often comparable. Due to the strong influence that the peat mosses have on their environment (to the extend that in most cases they form their own substratum), chemical and hydrological conditions do not differ too much even between continents. This is notably so when ombrotrophic mires are compared.

Some of the differences between countries might be nomenclatural rather than ecological. In Britain *Sphagnum capillifolium* (Ehrh.) Hedw. and *S. rubellum* Wils. are often treated as one species (Hill 1976) in contrast to most North American and Scandinavian sphagnologists who argue that they are separable and are different ecologically (e.g., Cronberg 1989, see also Andrus 1979). McQueen (1989) showed that differences in gametophyte morphology were largely environmentally induced, but spore morphology was little affected by environment and could be used to distinguish the taxa.

Also the *Sphagnum recurvum* group has been treated in different ways by different authors. (For example, see discussion on the ecology of *S. angustifolium* (Russ.) C. Jens. and *S. fallax* (Klinggr.) Klinggr. in Horton et al. 1979 and Vitt and Slack 1984.) I use the originally reported species names when referring to different studies in this paper.

This review deals with mechanisms that may help to understand why the species occupy a restricted part of the water-level gradient. The processes of formation of this gradient, in which properties of the dead mosses seem more important than those of the living ones, have recently been treated by Rochefort et al. (1990), Sjörs (1990), Vitt (1990), Johnson et al. (1990), and Johnson and Damman (1991). The last two papers are reviewed by Moore (1991).

Position of the Species Along Water-Level Gradients

Niche and habitat relations along water-level and other gradients have been described by a large number of authors. Since this review focuses on mechanisms, the aim of this short section is to point out some generalities and to indicate important literature in which the patterns are described in detail.

Hummocks are commonly formed by *Sphagnum capillifolium* (= *S. nemoreum* Scop.), *S. rubellum*, or *S. fuscum* (Schimp.) Klinggr. of sect. *Acutifolia*. Of these, *S. rubellum* grows at the lowest height and is often a lawn species. *Sphagnum fuscum* seems normally to reach the highest position, but *S. capillifolium* sometimes grows higher (e.g., Andrus et al. 1983) and is more important in shaded positions and in mire margins (Sjörs 1948, Fransson 1972, Horton et al. 1979). Where *Sphagnum* occurs in rich fens lawns and low hummocks are formed by *S. warnstorfii* Russ., and the hummocks are often capped by *S. fuscum*, which then grows at such a height that the plants are isolated from the mineral-rich high-pH water in the fen (e.g., Giller & Wheeler 1988).

The lower parts of the gradient are often dominated by species of sect. *Cuspidata*, including *Sphagnum angustifolium* (which also forms low hummocks (e.g., Vitt & Slack 1984)), *S. balticum* (Russ.) C. Jens., *S. cuspidatum* Hoffm., *S. fallax*, *S. majus* (Russ.) C. Jens., and *S. tenellum* (Brid.) Brid. (*Sphagnum tenellum* is sometimes placed in the monotypic sect. *Mollusca* (Daniels & Eddy 1985).) In the wettest hollows and along pool margins *S. cuspidatum* or *S. majus* often grow horizontally in floating carpets and thus experience an almost constant water level (Damman & Dowhan 1981, Rydin 1986).

Sphagnum magellanicum Brid. and *S. papillosum* Lindb. (sect. *Sphagnum*) occur over a wide range of water levels, e.g., in floating or semifloating

carpets (Sjörs 1948, Vitt & Slack 1975, Vitt & Bayley 1984), in lawns (Sjörs 1948, Clymo & Reddaway 1971, Vitt & Slack 1984, Rochefort et al. 1990, Vitt et al. 1990), forming hummocks on their own (Vitt, Crum & Snider 1975), or together with species of sect. *Acutifolia* (Ratcliffe & Walker 1958, Vitt, Achuff & Andrus 1975, Vitt & Slack 1984, Luken 1985, Gignac 1987). Several authors have demonstrated the wide height range of *S. magellanicum* within a mire (Vitt & Slack 1975, 1984; Damman & Dowhan 1981; Lane & Dubois 1981; Gignac 1987), and some studies even indicate a bimodal distribution of this species (Clymo & Hayward 1982, Økland 1986, Ilomets 1988).

In contrast, narrow ranges and especially a sharp upper limit, are characteristic of some hollow species. Examples are *Sphagnum cuspidatum* (Lane & Dubois 1981, Rydin 1986), *S. tenellum* (Økland 1986, Rydin 1986), and *S. pulchrum* (Braithw.) Warnst. (Damman & Dowhan 1981).

Details about the distribution of species along the vertical gradient, together with water-level data, can be found in Lumiala (1944), Ratcliffe and Walker (1958), Malmer (1962), Jeglum (1971), Vitt, Crum, and Snider (1975), Damman and Dowhan (1981), Lane and Dubois (1981), Bragg (1982), Clymo and Hayward (1982), Andrus et al. (1983), Boatman (1983), Vitt and Slack (1984), Økland (1986), Rydin (1986), Heikkilä and Löytönen (1987), Ilomets (1988), Vitt et al. (1990), and Gignac et al. (1991a, b). In most of these studies water level was measured only once. Data for water-level fluctuations and species position in relation to mean water level that could be compared between sites are available only in a few cases (Malmer 1962, Bragg 1982, Andrus et al. 1983, Boatman 1983, Økland 1986, Rydin 1986). Other sources of information on the habitat preferences of *Sphagnum* are Sjörs (1948), Sonesson (1970), Fransson (1972), Vitt, Achuff and Andrus (1975), Vitt and Slack (1975), Horton et al. (1979), Slack et al. (1980), Slack (1982, 1984, 1990), Daniels and Eddy (1985), Gignac and Vitt (1990), and Vitt and Chee (1990).

In any one mire there are often as many as half a dozen hollow species, and several of them grow in close contact without any obvious differences in habitat preference. Ilomets (1988) found up to four species in 1-dm^2 plots, and I have reported five species in 4-cm-diameter plots (Rydin 1986). Vitt and Slack (1975) found ten species of *Sphagnum* in a floating carpet community type with little variation in topography. Species richness in *Sphagnum* assemblages peaks at low or intermediate heights, but the pattern is quite variable (Fig. 1). Normally there are only one or two species at the top of a hummock. When there are more, there is often a strong dominance by one or rarely two. Where the studied gradient extends to levels that are inundated, the species richness often drops at this end too.

Species composition in bogs differs regionally, and especially important

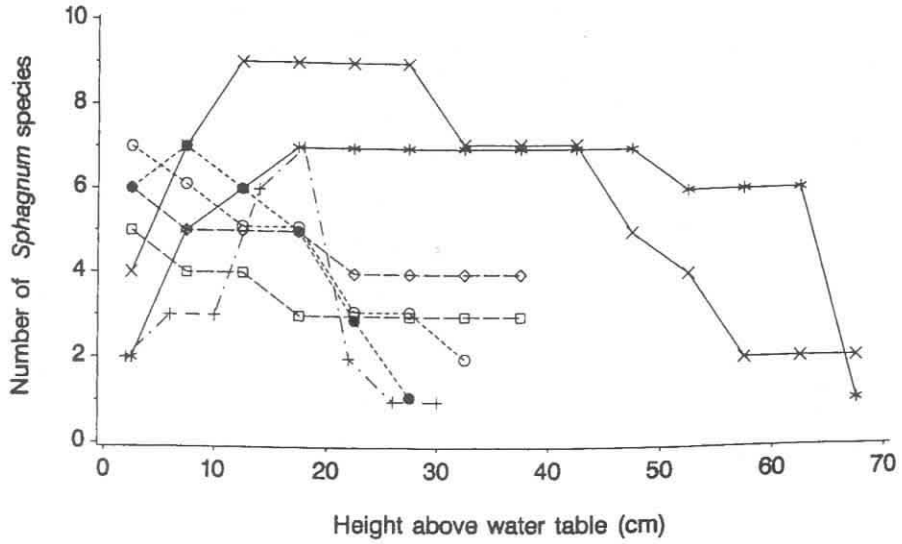

Figure 1. Number of *Sphagnum* species in relation to water table in *Sphagnum*-dominated peatlands. In most studies water level was measured only once and does not correspond to mean water level. Therefore, the curves were adjusted so that the lowest water level class starts at 0 cm. Number of species are given for 5-cm intervals (4-cm intervals for Kentra). (□– – –□) Nigula and (◊– – –◊) Männikjärve, raised bogs in Estonia (Ilomets 1988); (● - - - - - ●) Ryggmossen and (○ - - - - - ○) Kulflyten, raised bogs in southern central Sweden (Rydin 1986 and unpublished); (+— · — · —+) Kentra, a bog in north-west Scotland (Clymo & Hayward 1982); (✳—✳) Bloomingdale; and (×—×) Raybrook, poor fens in New York, U.S.A. (Andrus et al. 1983).

are the differences between oceanic and continental areas. Plants of species in sect. *Sphagnum* are, for instance, more often dominant hummock formers in oceanic areas (Horton et al. 1979). In Sweden *Sphagnum papillosum* grows in ombrotrophic mires in the southwest but is restricted to poor fens toward the east. In western Sweden *S. fuscum* is restricted to the highest hummocks, whereas in slightly more continental eastern Sweden *S. fuscum* also occupies the lower parts of the hummocks. In Canada Horton et al. (1979) showed that the oceanic hollow-to-hummock sequence, *S. cuspidatum* to *S. rubellum* to *S. papillosum*, is replaced in more continental areas by the sequence *S. jensenii* Lindb. to *S. angustifolium* to *S. magellanicum* (see also Vitt & Slack 1984). *Sphagnum molle* Sull. which grows in ombrotrophic mires in western Scandinavia is found in sites with at least some minerotrophic influence in Finland (Heikkilä & Lindholm 1988). Vitt et al. (1990) showed that *Sphagnum* species richness was higher in coastal

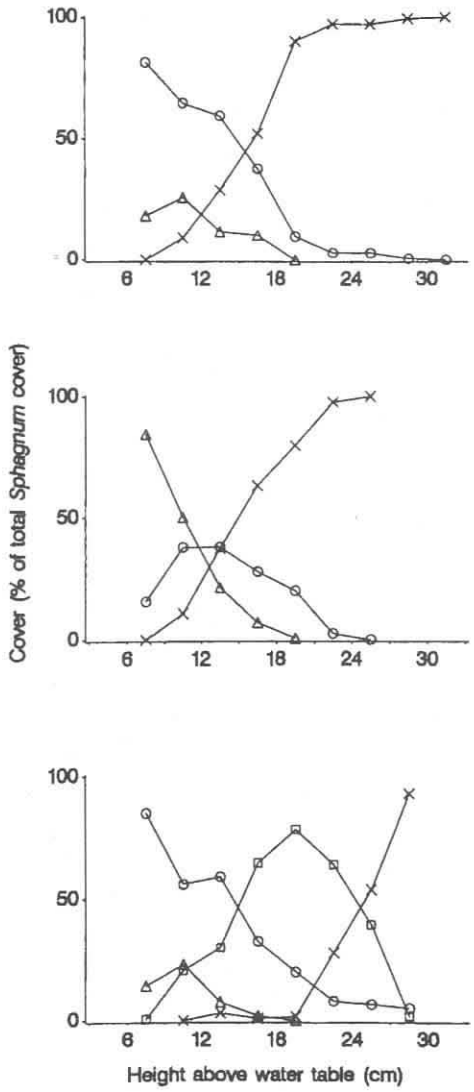

Figure 2. Relative cover of the most abundant *Sphagnum* species along the water-level gradient on Ryggmossen, Sweden. The species are ×, *S. fuscum*; ○, *S. balticum*; △, *S. tenellum*; □, *S. rubellum*. The three diagrams show how the distribution of species varies between different hollow-hummock transitions. The top diagram shows the most common transition type, with *S. balticum* dominating in the hollow; the middle one shows a transition in which *S. tenellum* co-dominates the hollows; the lower diagram shows a transition with *S. rubellum* (which is quite rare on this bog). (Redrawn from Rydin 1986.)

mires in British Columbia than in continental parts of Canada. An explanation for such differences could be that the concentration and composition of nutrients differ between oceanic and continental areas, although this has been questioned by Malmer (1988). Hydrological differences, such as the smaller annual range of water-table movement in oceanic areas, might be more important. This and other regional trends in

Sphagnum vegetation have recently been dealt with by Gignac (1989), Økland (1990b), Gignac and Vitt (1990), and Gignac et al. (1991a, b) in which references to older literature can be found.

Andrus et al. (1983) compared two sites (poor fens) in New York State, U.S.A. In one of them the water table dropped markedly during dry periods, and the mire was dominated by hummock formers. The other mire had a less variable water regime and fewer hummocks. The height distribution of *Sphagnum* was rather similar in these sites, when expressed as dominance in each height class. Ilomets (1988) also concluded that height distribution did not differ significantly between two Estonian bogs.

Within a mire the distribution along the water-level gradient might be affected by what species are present (Rydin 1986). This can be seen in a Swedish bog (Fig. 2) where *Sphagnum fuscum* is the dominant hummock species and *S. balticum* dominates the hollows. Where *S. rubellum* is present it truncates the lower range of *S. fuscum* but seems to have no effect on the vertical range of the hollow species. Where *S. tenellum* co-dominates the hollows, the lower but not the upper limit of *S. balticum* is affected.

Several other environmental variables vary together with the water-table gradient. Shading is often related to height (Gignac & Vitt 1990, Vitt et al. 1990). The classical phytosociological border between hummocks and hollows in northwestern Europe, the lower limit of *Calluna vulgaris*, reflects this. This ericaceous dwarf shrub, which lacks aerenchyma and is associated with mycorrhiza, cannot stand flooding for long periods (Malmer 1962). Experimental investigations comparing hummocks and hollows are often made at sites with minimal vascular plant cover to avoid confounding shading and height. There might be differences also in nutrient avail-ability, since Pakarinen (1978) and Malmer (1988) found that concentrations of N, P, and K were generally higher in hollow species than in hummock species. The rate of nitrogen fixation in organisms associated with *Sphagnum* is sometimes higher in hollows (Granhall & Selander 1973, Chapman & Hemond 1982), and variability in element concentration appears to be higher in the hollows (Aulio 1982). The pH may often increase from hummock to hollow (Vitt, Crum & Snider 1975). This trend is clearer in fens than in bogs, since in fens the hollows are in more direct contact with the minerotrophic water (e.g., Vitt, Achuff & Andrus 1975, Slack et al. 1980, Karlin & Bliss 1984). In the extreme case a calcareous rich fen may have high hummocks with low pH and ombrotrophic or near-ombrotrophic conditions (e.g., Giller & Wheeler 1988). Microclimate also differs. In Scotland Hulme and Blyth (1982) found that growth could continue longer in habitats closer to the water table, but in colder climates the hummocks become snow-free and start to thaw earlier than the hollows (Eurola 1968). In hummocks slope and aspect affect the temperature in the

capitula (Rydin 1984) but probably not species composition (Andrus et al. 1983).

General Features of the Species and Their Habitats

In this section I present evidence for a number of statements regarding the height that species occur above the water table. For convenience, I refer to them as hummock and hollow species to indicate their main habitat preference. The term hollow includes the lawns and the carpets (Sjörs 1948). The word shoot is used for a capitulum-bearing plant, and shoot density thus refers to numbers of capitula per unit area. The statements are presented with a few exceptions, but further research may well challenge their generality.

(1) Hollow species have a capacity for a higher growth rate than hummock species.

Numerous studies have shown that when species are studied in their natural habitat, or in the laboratory with plants taken from their typical habitat, growth is generally greater in species represented lower along the water-level gradient. This was shown by measuring photosynthetic rate (Johansson & Linder 1980, Titus et al. 1983, Silvola 1985) or growth in length or mass (Overbeck & Happach 1957, Clymo 1970, Clymo & Reddaway 1971, Pedersen 1975, Pakarinen 1978, Hulme & Blyth 1982, Hayward & Clymo 1983, Wieder & Lang 1983, Luken 1985, Austin & Wieder 1987, Wallén et al. 1988, Moore 1989).

Some published results differ from the general pattern. Lindholm and Vasander (1990) found that, although growth in length and relative growth rates were very low in the hummock species *Sphagnum fuscum*, its populations had a high volumetric and shoot density. Therefore the production per unit ground area was sometimes high. Rochefort et al. (1990) reported the usual production ranking in a bog (or at least a near ombrotrophic mire), but in a poor fen the production of *S. fuscum* hummocks was higher, and also higher than in the lawns and carpets (see also Bartsch & Moore 1985 and Vitt 1990).

Clymo and Hayward (1982) cited typical productivity values from British bogs to be 150, 500, and 800 g m^{-2} yr^{-1} for hummocks, lawns, and pools, respectively. Moore (1989) found an average difference of about 100 g m^{-2} yr^{-1} between hollows/lawns and hummocks in a review of the literature. There was, however, a large scatter in the data, some of which could be attributed to climate, but differences in methods and variation between years also contributed to the variability. Lists of published productivity estimates were recently compiled by Lindholm and Vasander (1990) and Rochefort et al. (1990).

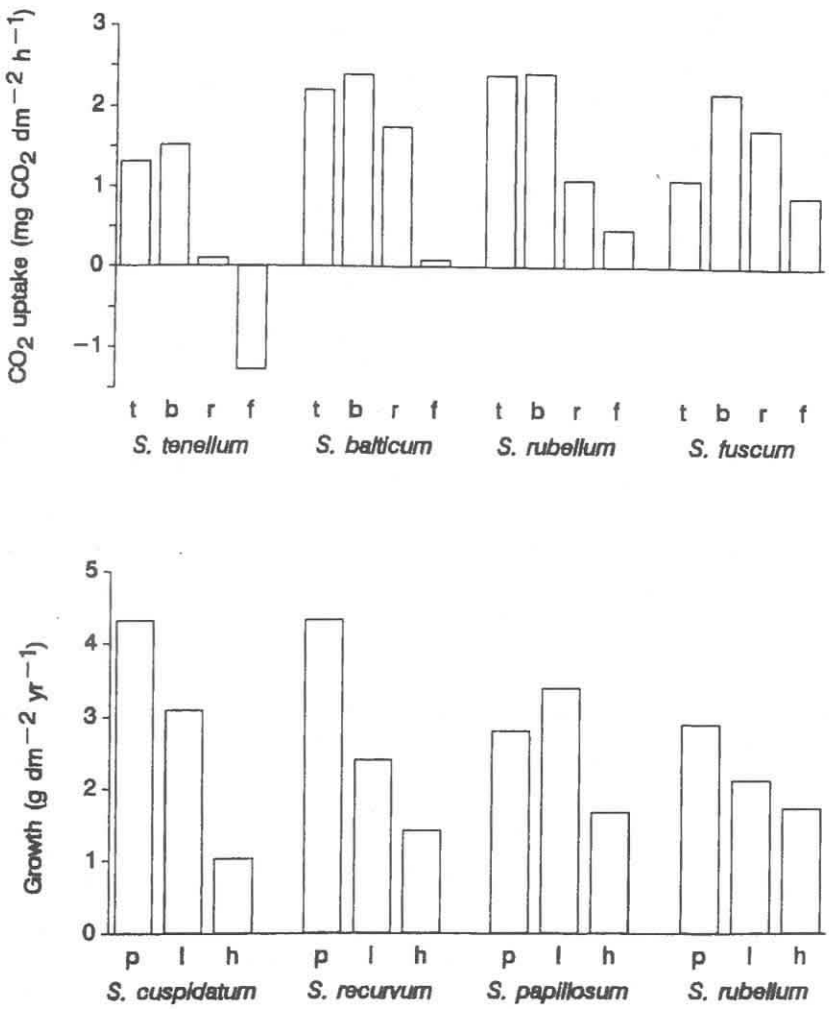

Figure 3. The effect of transplanting *Sphagnum* to different positions with reference to the water table. The species are arranged from left to right in the order they occur in a hollow to hummock gradient. The habitats are also arranged from the lowest to the highest. In the top diagram (redrawn from Rydin & McDonald 1985a) the habitats are t, *S. tenellum*; b, *S. balticum*; r, *S. rubellum*; f, *S. fuscum*. Samples of the transplants were collected after three months and the CO_2 uptake measured at wet state and at saturating light level. In the lower diagram (redrawn from Clymo & Reddaway 1971) the habitats are p, pool; l, lawn; h, hummock. The response was measured as annual growth.

It is not always possible in these studies to separate the effect of species from that of habitat, but Johansson and Linder (1980) found that *Sphagnum balticum* always had higher rates of photosynthesis than *S. fuscum*, whether growing separately or mixed together. When growth is measured under different conditions, i.e., in different habitats or in different years, the capacity for growth (under optimal conditions) is highest in hollow species (Clymo & Reddaway 1971, Titus & Wagner 1984, Moore 1989).

(2) All species grow as well or better in hollows than in hummocks, whereas hollow species are unable to grow much higher than their natural habitat.

Johansson and Linder (1980) found that *Sphagnum fuscum* and *S. balticum* had a higher rate of photosynthesis in wetter habitats. Clymo and Reddaway (1971) showed in a transplant experiment that *S. recurvum* P. Beauv., *S. papillosum* and *S. rubellum* had higher growth in length and dry mass in lawns than in hummocks (Fig. 3). When patches of a hollow species were placed high above the water table, the plants showed a decreased growth rate (Clymo & Reddaway 1971; see also Clymo 1970). If the treatment is drastic the plants die. Large parts of *S. balticum* and *S. tenellum* lawns grown at a constant level of 15 cm above the water table or transplanted to a *S. fuscum* hummock died within a few years (Rydin 1986). Clymo (1970) also observed death of *S. cuspidatum* and *S. recurvum* on hummocks. No mortality could be observed in *S. fuscum* transplanted to hollows (Rydin 1986), but the plants seemed to suffer from very wet treatments (such as at the water table in a pool).

In addition to these direct effects of habitat on growth, environmental conditions also affect the morphology of the shoots. Hayward and Clymo (1983) and Li et al. (1992) found that growth in length generally increased when the water table was closer to the surface but that water table had little effect on growth of mass. With higher water levels the shoots were usually more slender. The mats are often less dense closer to the water table. This allows light to penetrate further (Overbeck & Happach 1957, Clymo & Hayward 1982) and a longer part of the shoot to be photosynthetically active (Johansson & Linder 1980).

Another effect of habitat on physiology is that both hollow and hummock plants growing naturally or experimentally near the water table show a higher photosynthetic rate when brought into standard conditions in the laboratory than do plants grown at a higher level (Fig. 3; Rydin & McDonald 1985a). An *in vitro* experiment by Wallén et al. (1988) gave slightly contradictory results. They suggested that optimum for growth was 20 cm above the water table for *Sphagnum fuscum* and *S. rubellum* together and 10 cm for *S. magellanicum*. However, the trends were not clear, and the measurements were made in a rather artificial way. In fact *S. fus-*

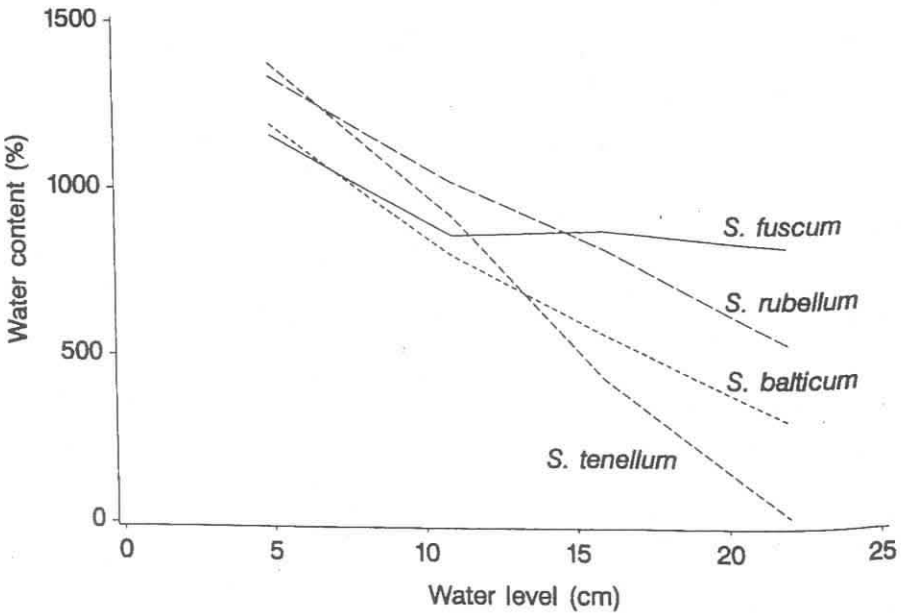

Figure 4. Water content in the capitula of four *Sphagnum* species as the water table was artificially lowered from 5 to 22 cm below the surface. (Redrawn from Rydin 1986.)

cum and *S. rubellum* had their highest photosynthetic rate per unit dry mass when grown at 5 cm above the water table.

(3) Hummock and hollow species differ in their water transport ability.

When *Sphagnum* shoots are saturated with water (e.g., during and after rain), the water content could be 20 times the dry mass or more. As water content decreases to 10–30% of dry mass, the shoots become whitish and fragile. When the water table sinks during periods without rain, the capitula (where most of the photosynthesis takes place) lose water by evaporation, and this water is replaced from below.

Water transport takes place in an external capillary network between leaves, branches, and stem and branches. Hayward and Clymo (1982) found that the hummock species, *Sphagnum capillifolium*, had more capillary spaces for this purpose than did *S. papillosum*, which grows closer to the water table. At any given height above the water table, the water content of capitula was higher in *S. capillifolium* than in *S. papillosum*. For four species compared by Rydin (1985), the water content in the capitula was ranked as *S. fuscum* > *S. rubellum* > *S. balticum* > *S. tenellum* as the water

table was lowered experimentally to 22 cm below surface (Fig. 4). This order is the same as that of the uppermost levels reached in a hummock by the four species.

In addition to a differential ability to transport water it is likely that evaporation rate per unit ground area is lower in hummock species. With their dense and often very smooth surface, the evaporating area is probably smaller than that in hollow species. Reflecting this, Overbeck and Happach (1957) found that evaporation was higher from *Sphagnum recurvum* (hollows) than from *S. rubellum* (hummocks) when water table was close to the surface. However, the opposite relation between hummock and hollow species was reported by Clymo (1973). Both investigations showed that evaporation was reduced as the water table was lowered and that reduction was smaller in the hummock species, which probably was an effect of their better water-transport ability. However, Nichols and Brown (1980) found that evaporation from *S. recurvum* was similar, with the water table 5, 10, and 15 cm below surface. These somewhat conflicting reports were based on experiments with containers in a glasshouse, growth chambers, or outdoors and may not properly reflect the field situation. Nichols and Brown (1980) used peat cores cut from the mire, whereas Clymo (1973) and Overbeck and Happach (1957) used containers packed with shoots to approximate natural density. Detailed field studies of evapotranspiration (e.g., Bragg 1982, Roulet & Woo 1986) have not addressed the question of species differences. In growth chamber experiments evaporation from *S. recurvum* was about twice that from a free-water surface and increased 92% as temperature increased from 9 to 25°C (Nichols & Brown 1980). Presence of a vascular plant overstory did not affect evaporation but prevented some surface desiccation (Nichols & Brown 1980; cf. Brock & Bregman 1989).

Within species, capillarity can be affected by the fact that shoot size is smaller (i.e., capitulum density is higher) the higher the position above the water table. This has been shown in a number of species (Smolyanitsky 1977, Luken 1985, Haig 1989). Morphology changes with water level, and such changes affect water transport. Li et al. (1992) found that the branch leaves became shorter in shoots grown at 0 cm than at 10 cm above the water table, but generally the leaves were longer when the shoots grew closer to the water table (Nyholm 1969). Fascicle density increased with increasing distance above the water table in *Sphagnum imbricatum* Russ. (Green 1968) and in *S. magellanicum* and *S. papillosum* (Li et al. 1992). However, Smolyanitsky (1977) found the reverse pattern in *S. magellanicum*. From the results of Li et al. (1992) it is clear that a lower fascicle density close to the water table was partly a result of a greater growth in length, but it also appeared that fewer fascicles were initiated per unit time. Under

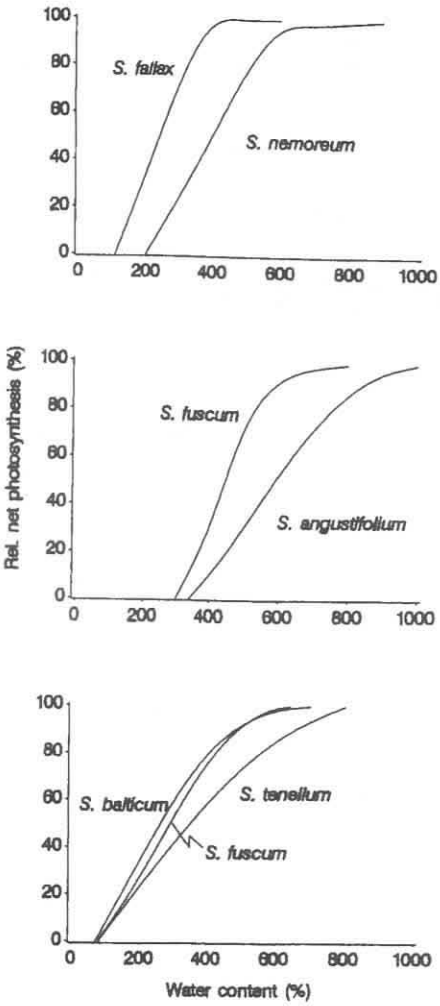

Figure 5. Net photosynthesis (expressed as CO_2 uptake as percentage of maximum) in relation to water content. (Redrawn from Titus et al. 1983, top; Silvola & Aaltonen 1984, middle; Rydin & McDonald 1985b, bottom.)

experimental conditions more slender shoots were produced with the water table close to the surface than with the water table lower (Hayward & Clymo 1983). Similarly, Brock and Bregman (1989) found that *S. recurvum* growing in a *Betula* carr formed more slender shoots in a wet year (with the water table near to the surface) than in a dry year.

(4) Photosynthesis is reduced at lower water content, but there is no evidence that hummock and hollow species react differently.

Water content has a profound effect on photosynthesis (Grace 1970, Skre & Oechel 1981, Titus et al. 1983, Silvola & Aaltonen 1984, Rydin & McDonald

1985b, Gaberščik & Martinčič 1987, Murray et al. 1989). Silvola and Aaltonen (1984) found that the hummock species, *Sphagnum fuscum*, maintained higher photosynthesis at reduced water content than did the hollow species, *S. angustifolium*. However, Titus et al. (1983) found the opposite relation between the hummock and hollow species when comparing *S. nemoreum* Scop. and *S. fallax*. Rydin and McDonald (1985b) detected no difference between *S. fuscum* (hummock) and *S. balticum* (hollow) but found *S. tenellum* (hollow) to be slightly more sensitive to reduced water content (Fig. 5).

The water content at which the rate of photosynthesis dropped differed among investigations, which probably is due to differences in the methods employed. Titus et al. (1983) monitored photosynthesis and water content in shoots 5 cm long, whereas Silvola and Aaltonen (1984) used 1–1.5-cm-thick patches. With 5-cm-long shoots, it is likely that water content is higher in the lower parts of the shoots, but these parts may not be reached by light. Different species may differ in the amount of water held by the lower parts of shoots. Rydin and McDonald (1985b) used capitula spread out in a petri dish. In this way water content is measured in the tissue where photosynthesis takes place and indicates that maximum net photosynthesis is reached at 600–800% of dry mass (cf. Silvola 1985) and is reduced to 50% of this maximum at 200–300% water content. At water contents above 800–1000% the rate of photosynthesis drops, probably as an effect of increased resistance to CO_2 diffusion (Silvola 1985).

(5) Hollow species are more often and more severely desiccated in the field than are hummock species.

This is the consequence in the field of point (3). After a period of dry weather, and consequently a lower water table, capitula in the carpets and lawns begin to dry out long before those of the hummock formers do so. This has been shown in studies covering a range of regions and species: *Sphagnum rubellum, S. magellanicum,* and *S. recurvum* (Overbeck & Happach 1957); *S. capillifolium* and *S. recurvum* (Bragg 1982); *S. nemoreum* and *S. fallax* (Titus & Wagner 1984); *S. fuscum, S. magellanicum,* and *S. angustifolium* (Luken 1985); *S. fuscum, S. balticum, S. tenellum,* and *S. rubellum* (Rydin 1985, Rydin & McDonald 1985b) *S. rubellum, S. balticum,* and *S. tenellum* (Heikkilä & Löytönen 1987); and *S. rubellum/S. fuscum* and *S. magellanicum* (Wallén et al. 1988).

Thus, although the hollow species grow nearer the water table and are often flooded or water saturated, photosynthesis in them is more often limited by desiccation than in hummock species. Therefore, hollows may, paradoxically, be viewed as the drier of the two habitats. To find *Sphagnum tenellum* and *S. balticum* papery white in hollows is quite common; to find *S. fuscum* dry even on the highest hummocks is an unusual event (Rydin & McDonald 1985b, Rydin 1986).

Table 1. Annual growth and production of *Sphagnum fuscum* and *S. angustifolium* in a wet and a dry year. Data from Luken (1985) are given with standard error in parentheses.

	annual growth			wet/dry
	wet year	dry year	unit	ratio
Bog forest, Luken (1985)				
S. fuscum	4.3 (0.5)	2.4 (0.2)	mm yr^{-1}	1.8
S. angustifolium	11.3 (1.1)	1.3 (0.1)	mm yr^{-1}	8.7
Andromeda bog, Luken (1985)				
S. fuscum	8.2 (0.7)	4.7 (0.4)	mm yr^{-1}	1.7
S. angustifolium	22.3 (2.9)	9.1 (1.3)	mm yr^{-1}	2.5
Poor fens, Moore (1989)				
S. fuscum	75.3	83.5	g m^{-2} yr^{-1}	0.9
S. angustifolium	127.4	29.2	g m^{-2} yr^{-1}	4.4

Since moisture conditions are crucial for the annual growth of *Sphagna* (Backéus 1988, Murray, Tenhunen & Kummerow 1989, Lindholm 1990), and since hollow species dry out more quickly than hummock species, dry years will reduce the growth in hollow species more than in hummock species, sometimes to the extent that growth in the hollows is lower than in the hummocks (Table 1). Results from growth studies in a single year must be interpreted cautiously (Clymo & Reddaway 1974, Rochefort et al. 1990, Vitt 1990). In a *Betula* carr, where the trees gave some desiccation protection, Brock and Bregman (1989) found that production in *Sphagnum recurvum* var. *mucronatum* (Russ.) Warnst. differed little between a dry and a wet year, but growth in length was greater in the wetter year.

(6) There is no evidence of any general difference in desiccation tolerance between hummock and hollow species.

Drying out may cause damage to the plants and even be lethal, but few comparisons have been made of the ability of hummock and hollow species to survive and recover after desiccation. Wagner and Titus (1984) showed that the hollow species, *Sphagnum fallax*, recovered better and after longer periods of desiccation than did the hummock species *S. nemoreum*, but Clymo (1973) investigated seven species and concluded that there was no correlation between desiccation tolerance and the wetness of the species' natural habitat. For instance, the tolerance of the hummock species *S. rubellum* was very similar to that of the pool-inhabiting *S. cuspidatum*.

Photosynthetic rate will be lower after re-wetting from the dry state, which may relate to reduced chlorophyll content (Wagner & Titus 1984, Gaberščik & Martinčič 1987). The net loss of assimilates at re-wetting is suggested to be the factor that limits the desiccation frequency that bryophytes can tolerate (Proctor 1982). However, it seems that no one has

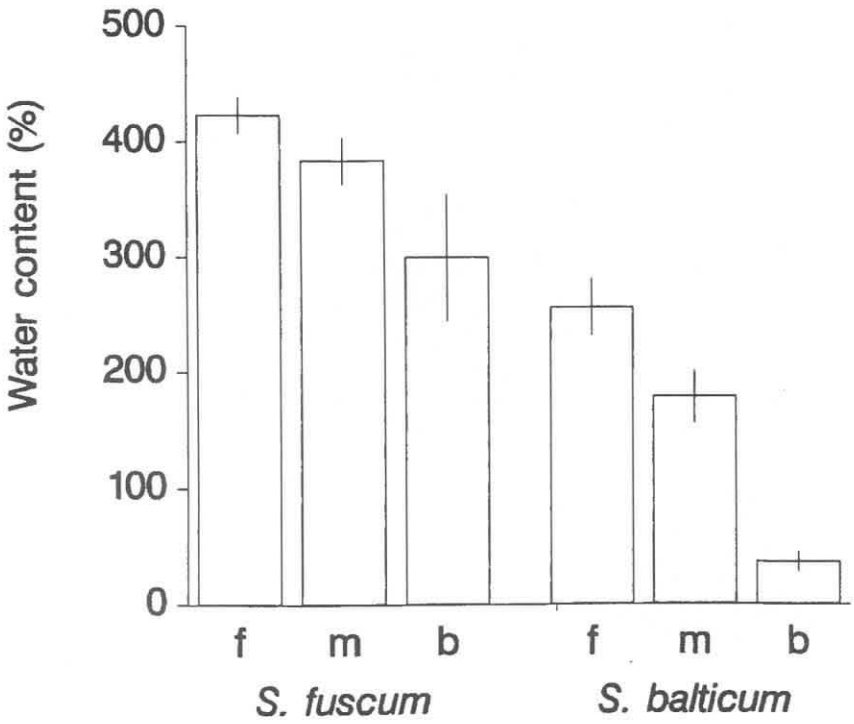

Figure 6. Water content in capitula of *Sphagnum fuscum* and *S. balticum* in a mixed lawn after experimental drying. Water content was measured separately for shoots surrounded by f, *S. fuscum*; b, *S. balticum*, or m, a mixture of the two species. Error bars represent ± one standard error. (Redrawn from Rydin 1987.)

measured what might be the most important ecological aspect of drought: the ability to recover after repeated desiccation.

(7) Well above the water table, shoots of hollow species benefit from being surrounded by shoots of hummock species.

Although patches of a hollow species will become dry more quickly than patches of the hummock species, there will be some lateral (i.e., between shoot) movement of water, and shoots of hollow species that are surrounded by shoots of hummock species will maintain a higher water content than shoots growing in a single species patch at the same height. This effect has been demonstrated by field measurements after a period of dry weather and by laboratory experiments. In a study of *Sphagnum fuscum*, *S. balticum*, *S. tenellum*, and *S. rubellum* (Rydin 1985, 1987), the most

marked effect was that of *S. fuscum* on *S. balticum* (Fig. 6). In the mire studied *S. balticum* was found to occur almost to the top of most hummocks, but it showed an increasing degree of contact with shoots of *S. fuscum*. There was also a positive effect of *S. rubellum* on the water content of *S. balticum* shoots, and of *S. balticum* on *S. tenellum*, but *S. fuscum* and *S. rubellum* seemed to have no effect on each other. Their ability to keep moist is rather similar (Rydin 1985). Heikkilä and Löytönen (1987) also found field evidence for a positive effect of *S. rubellum* and *S. balticum* on *S. tenellum*. Titus and Wagner (1984) measured a positive effect of *S. nemoreum* on *S. fallax*, and Li et al. (1992) reported a positive effect of *S. magellanicum* on *S. papillosum*. I have proposed that the effect on the hummock matrix is negligible and used the term "commensalism" for this interspecific relation (Rydin 1985). Titus and Wagner (1984) wrote that the interaction "may or may not significantly influence *S. nemoreum* plants in an encompassing matrix," but nevertheless they used the term "piracy" to describe the relationship.

(8) Hummock species have a higher cation-exchange capacity than hollow species.

The ability of *Sphagnum* shoots to acidify the substratum by cation exchange is reviewed in Clymo and Hayward (1982) and Andrus (1986). The ecological importance of species differences is not clear, but the higher exchange capacity of hummock species (Clymo 1963, Vitt, Crum & Snider 1975) than hollow species coincides with the sometimes observed decrease in pH with increasing height above the water table (Vitt, Crum & Snider 1975).

Interactions Among *Sphagnum* Species

By transplanting a small patch of one species into positions occupied by plants of another species, it is possible to monitor interspecific competition along gradients. *Sphagnum* vegetation forms a monolayer, and I have viewed the interactions between individual shoots as interference competition for space, since the occupation of an area by one shoot precludes its occupation by another (Rydin 1986, 1993; see also Slack 1990). The monolayer is maintained by forces acting on individuals. Shoots growing more rapidly in length than their neighbors will be more prone to desiccation, which leads to diminished growth (Smolyanitsky 1977, Hayward & Clymo 1983). In dense mats (such as those formed under full sun) the euphotic zone is normally not more than 1-2 cm deep (Clymo & Hayward 1982, Rydin & McDonald 1985a), and etiolation prevents a shoot from growing less in length than its neighbors. It follows that shoots with lower

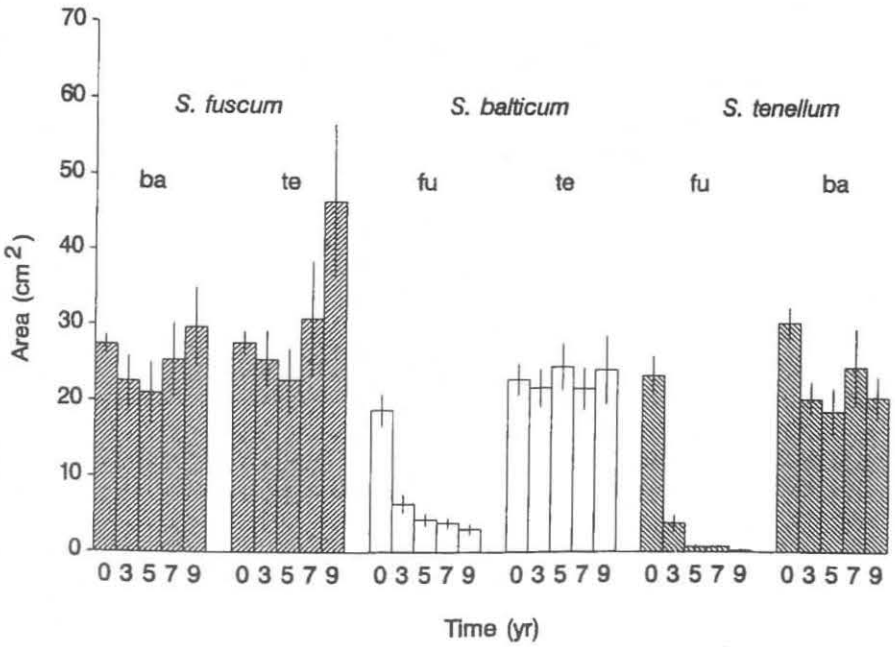

Figure 7. Change in area of patches of *Sphagnum fuscum*, *S. balticum*, and *S. tenellum* reciprocally transplanted, after three, five, seven, and nine years. The abbreviations indicate the habitat into which the species was transplanted (ba, *S. balticum*; te, *S. tenellum*; fu, *S. fuscum*). Error bars represent ± one standard error. (From Rydin 1993.)

growth in mass must remain slender to keep their position in the moss surface and that therefore they will cover a smaller part of the surface area. In the extreme case such shoots will be overtopped and buried. The outcome of interspecific competition can thus be measured as the change in surface area occupied by shoots of the competing species.

Experiments in which patches of the hummock species, *Sphagnum fuscum*, and two hollow species, *S. balticum* and *S. tenellum*, were reciprocally transplanted were started in 1979–1983. The results after five and eleven years were evaluated (Rydin 1986, 1993). The main results are summarized in Figure 7.

A small patch of a hollow species placed in a hummock will invariably decrease in area, not because of competition with *Sphagnum fuscum*, but as a result of mortality. This result seems to relate to the inferior water transport capacity of the hollow species and agrees with findings by Lopatin (1954) and Clymo (1970). The long-term results also agree with predictions

made from water balance measurements (Rydin 1985), namely once *S. balticum* has suffered initial mortality (over ca. three years), the remaining individuals can survive very high on the hummocks because they are provided with water from the surrounding *S. fuscum* matrix. Since growth of *S. balticum* requires contact with *S. fuscum*, it is unable to increase its area in these patches. *Sphagnum tenellum*, which has a poor water transport ability, was eliminated from several hummocks.

When a patch of *Shagnum fuscum* was grown in the habitat of a hollow species, initial results (Rydin 1986, and three to five year results in Fig. 7) showed a decline in its area. This is the expected result from what is known about the growth rate of the species involved (see (1) in previous section). This seems to agree with the general view that, since hummock mosses can tolerate the hollow environment but do not normally grow there, they are excluded by competition from the faster growing hollow species (Clymo & Reddaway 1971, Clymo & Hayward 1982, Titus & Wagner 1984, Rydin & McDonald 1985a, Andrus 1986, Rydin 1986, Økland 1990a). After seven to nine years, however, *S. fuscum* had recovered, and on average had even increased in area in the habitat of the hollow species. Water levels for these transplants were at the modes of the hollow species, *S. balticum* and *S. tenellum*, i.e., about 10 cm above mean water table. (Treatments did not include the lowest parts of the hollows.) *Sphagnum fuscum* occurs only infrequently at this height (Fig. 2). These experiments give no support to the view that it is competitively inferior to the hollow species. I have earlier noted (Rydin 1986) that when *S. fuscum* was grown close to the water table it suffered some mortality, and the patches were invaded by algae. Therefore, the very lowest levels at which *S. fuscum* can grow may be set by intolerance to flooding rather than by competition (also suggested by Kivinen 1948 *non vide*, cited in Silvola & Aaltonen 1984). The summer rainfall during the study period was slightly higher than average, but long periods with unusually high water levels may be more critical for the long-term survival of *S. fuscum* in the hollows.

Sphagnum balticum and *S. tenellum* represent a case of hollow species with overlapping habitat niches, the range of *S. tenellum* being included in that of *S. balticum* (Fig. 2). The initial evaluation showed *S. balticum* to have a slight competitive advantage (Rydin 1986). However, as shown in Figure 7, *S. balticum* neither loses nor wins area from *S. tenellum* in the *S. tenellum* habitat, but it does on average win area in its own habitat. This trend, however, was reversed in one year (1989), when *S. tenellum* gained area in all experimental plots and also in permanent nonexperimental plots (Rydin 1993). It is unclear what features of the weather that year favored *S. tenellum*.

There was also phenological variability, with *Sphagnum tenellum* often

gaining area in the late summer and autumn and *S. balticum* in the early summer (Rydin 1993). Different periods of growth were reported by Li et al. (1992), with peaks in mass formed in months with high precipitation in *S. papillosum* and in drier months in *S. magellanicum*. These two species also differed in their response to photoperiod (Li & Glime 1991). There seems also to be seasonal variability in photosynthetic response to drought (Titus et al. 1983). Chlorophyll content varies seasonally, possibly in different ways in different species (Spatt 1978, Haig 1989, Gaberščik & Martinčič 1987). Johansson and Linder (1980) suggested that species might differ in their diurnal pattern of photosynthesis, possibly as a result of differences in the light compensation point.

The behavior of *Sphagnum tenellum* in the habitat of *S. balticum* was more variable than that of *S. balticum* placed in *S. tenellum* habitat. The structure of the surface peat often differs between sites on which these species grow. Shoots of *S. balticum* often remain intact downward for 8–12 cm, whereas shoots of *S. tenellum* are often disintegrated at a depth of 3–5 cm where the underlying peat is highly humified. The fate of transplants of *S. fuscum* in the hollows also showed high variability, perhaps due to differences in the underlying (but close to the surface) peat structure, the often inhomogeneous pattern of desiccation in the carpet, or the variability in growth between replicates in what appears to be a uniform habitat (see discussion in Clymo & Hayward 1982 and Boatman 1983).

Another pair of species with highly overlapping vertical ranges, *Sphagnum magellanicum* and *S. papillosum*, was compared by Li et al. (1992) who reported that the species grew better in mixtures than in monocultures, thus suggesting an interaction involving protocooperation rather than competition. The experiments were made with artificially assembled mixtures, and since the arrangements of shoots and thus light penetration and water balance, might affect this result, it would be interesting to obtain results from natural mixtures.

I have in progress competition experiments under constant (growth chamber) conditions between *Sphagnum fuscum*, *S. balticum*, and *S. tenellum* with the water table close to the surface. Although it is difficult technically to run such experiments for a long time (because the surface of the shoots do not stay horizontal), these experiments were set up to reduce variability and to create a situation in which competitive advantage of a species would most likely be expressed. Titus and Wagner (1984) on the basis of unpublished data stated: "In laboratory and field experiments, *S. fallax* consistently overtopped *S. nemoreum* in mixed patches when the water table was high." Boatman and Tomlinson (1977) observed *S. cuspidatum* shoots lying horizontally across a wet carpet of *S. papillosum* and reasoned

that "where the shoots become sufficiently dense it is possible that they can smother and kill *S. papillosum* locally."

Haig (1989) created artificial hummock-hollow zonations with *Sphagnum capillifolium*, *S. papillosum*, and *S. recurvum* in inclined boxes in which the plants were arranged in parallel bands from the water table to the "hummock." When the boxes were rotated 90°, the plants started immediately to re-establish themselves closer to their natural position relative to the water table. This was partly due to *S. recurvum* "slumping" to the lower parts, and also its ability to grow horizontally in very wet situations (a habit that allows each shoot to occupy a larger area). It was not determined whether *S. capillifolium* in the end would consistently disappear from the wetter parts of the gradient.

Regeneration and Population Processes in *Sphagnum*

A species can gain surface area at the expense of others with which it is growing by increasing shoot size or producing more shoots, and species differences in sexual or asexual reproduction may therefore influence competitive ability. Vegetatively produced new shoots, often referred to as innovations, are suggested to arise from the stem at a fascicle (Baker & Boatman 1985, 1989). It is easy to demonstrate that if the apex of a shoot is damaged, an innovation from below will be formed that replaces the old capitulum. Smolyanitsky (1977) suggested that this might happen after severe desiccation and physical damage. There are dormant buds in the stem and branches below the capitulum, and they are probably kept at rest by hormonal control or by lack of oxygen and light (Karunen & Kälviäinen 1985, Clymo & Duckett 1986). That the potential for hormonal control exists is demonstrated by the rather efficient internal transport of metabolites that can take place in *Sphagnum* stems (Rydin & Clymo 1989). This transport is independent of the external transport of water.

Lane (1977) described the proportion of shoots bearing innovations for several species, but such data cannot be used comparatively unless growth rates are known. A characteristic feature of some species is their ability to form large numbers of tiny side shoots, which start as indeterminate branches a few cm below the surface and eventually reach the surface where each one can form a capitulum. Lane (1977) called these shoots "juvenile forms", and noted that they were common in hollow species such as *Sphagnum cuspidatum*. They are also characteristic of *S. tenellum* (Rydin unpublished). It is not known what ecological importance they might have.

The work of Boatman (1977, 1983) suggests that innovation frequency relates to habitat characteristics. It is known that various chemical factors

can promote branching (innovation formation) in *Sphagnum*. Baker and Boatman (1990) demonstrated this effect with N, P, K, and CO_2 and suggested that levels of P might limit vegetative reproduction in the field. However, it is known how these factors vary within a *Sphagnum* mat and whether this potential variation causes only some shoots to branch. Innovation frequency probably varies seasonally (Sobotka 1976), but it does not appear that differences in innovation frequency are genetic (Baker & Boatman 1989).

Apart from the effect of light and water balance that results in shoots staying in a monolayer, relatively little is known about how shoots respond to intraspecific competition. Haig (1989) studied shoot populations of *Sphagnum capillifolium*, *S. papillosum*, and *S. recurvum*. He found that *Sphagnum* can respond to artificial thinning by reduced shoot mortality, but his analyses did not suggest that the −3/2 thinning rule applies to *Sphagnum*. Haig (1989) also studied the fate of individual shoots from series of photographs taken at 2-week intervals over 15 months. His results suggest considerable flux in the *Sphagnum* populations. As is often the case with vascular plants (Harper 1977), most of this flux takes place during the summer when the growth rate is highest. Some shoots disappear by being overgrown, and it is suggested that this happens with a higher probability for smaller shoots surrounded by larger shoots. Other shoots may successfully produce new shoots by branching, and the chance for doing this increases with capitulum size. There also might be a link between biomass increase and vegetative reproduction. Li et al. (1992) reported a correlation between growth in mass and branching frequency in *S. magellanicum* and *S. papillosum*, and Clymo and Hayward (1982) also showed that capitula of *S. papillosum* divided more frequently in less dense populations (i.e., those with larger shoots). However, the relation between shoot production and shoot size does not seem to be very strong, indicating the importance of other factors. Baker and Boatman (1989) stated that innovation frequency was not related to capitulum size in *S. cuspidatum*. Differences between these species are expected because of their different growth forms. *Sphagnum cuspidatum* often grows in lax, sometimes floating carpets, in which a long section of each shoot reaches the surface, whereas *S. papillosum* forms dense mats with only the capitula reaching the surface. It might be expected that the capitulum has a stronger impact on the shoot in *S. papillosum*.

The success of a *Sphagnum* species may also depend on its ability to colonize patches with dead mosses, bare peat, or liverworts that are always present in mires. Bayfield (1976) demonstrated that *S. papillosum* can establish itself effectively from vegetative fragments. Species-specific differences in lateral growth rate or the ability to colonize by fragments

could be important, but spore establishment seems in general unlikely in bogs (Rydin 1986). Phosphate concentration in bog water has been stated to be too low for the growth of *Sphagnum* protonemata (Boatman & Lark 1971), and in submerged conditions the further development of the shoots may be CO_2 limited (Baker & Boatman 1985, cf. Paffen & Roelofs 1991). However, the work by Clymo and Duckett (1986) showed that protonemata can develop from spores or vegetative fragments in peat samples without addition of nutrients. It may be that some species are more capable of dispersal and colonization by spores than others. McQueen (1987, 1989) found a lower demand of calcium and phosphate in protonemata of *S. subtile* (Russ.) Warnst. than in *S. rubellum* and *S. capillifolium*. *Sphagnum lindbergii* Schimp. in Sweden is mainly a northern species, but it occurs in scattered localities, many of them in water-filled, disused peathags in the south, indicating long-distance dispersal (Sjörs 1949). Foster (1984) gave examples of *S. lindbergii* encroaching on bare peat and of *S. fuscum* overgrowing *Cladonia* on hummocks. Økland (1990a) suggested that *S. tenellum* is an efficient colonizer of bare peat, and he holds it to be more of an R-strategist (*sensu* Grime 1979) than either *S. balticum* or *S. fuscum*. Similar ruderal characteristics have been attributed to *S. molle* and *S. compactum* DC. (Heikkilä & Lindholm 1988, Slack 1990).

Conclusions

We now have some understanding of why the hollow species have an upper limit on the hummocks. The capitula dry out more often and more quickly than do capitula of the hummock formers. The main mechanism, differential water transport ability, is well documented, and we also know that this is linked to morphological differences that influence the effectiveness of the external capillary network of the shoots. The positive interspecific effect of the hummock-species matrix that enables single shoots of a hollow species to grow at a high level above the water table is also documented by several independent researchers. Again, the mechanism, lateral water transport, has been demonstrated both in field and laboratory studies.

We are much farther away from understanding the reasons for the lower limit for plants of the hummock species. The often found difference in growth rate has led to the conclusion that they are competitively excluded from the hollows. There is some experimental evidence for this, and Økland (1990a) consequently suggested that *Sphagnum* assemblages along the water gradient exemplify a competitive hierarchy (*sensu* Keddy 1989), with the strongest competitors dominating in the most favorable environment (the hollows).

However, the most recent study (Rydin 1993) does not support this view. Instead the species seem to differ little in competitive ability. This would agree with Keddy's assumption (1990) that closely related similar taxa could be expected to be competitive equivalents, but more research is needed to test whether this is indeed a generality. Also contrary to the competitive hierarchy model is the fact that along the gradient species richness is highest where productivity is highest, whereas in the model a dominant species is suggested to monopolize the most favorable environment.

We have so far no answer to the question how so many *Sphagnum* species can coexist in lawns and carpets seemingly without any habitat differentiation. Several of these species are morphologically similar, and remaining mechanisms include the phenological and regeneration niches (*sensu* Grubb 1977). Are the observed differences in growth rate and competitive ability between seasons and between years sufficient to explain the situation as a non-equilibrium coexistence? Can random events or species differences in establishment from spores or vegetative reproduction be sufficient to maintain species diversity? What is the siginificance of the observed spatial variability in growth rate, desiccation, and mineral concentration?

Clearly, these are several topics that deserve attention by experimentalists. Some of them pertain to the hummock-hollow question, but they are also of more general importance for an understanding of *Sphagnum* biology. In this paper I have noted the conflicting results on species differences in evapotranspiration and in morphological changes with height above the water table. This shows that there is room for more research on phenotypic plasticity and its ecological consequences in *Sphagnum*. There are old studies describing and even classifying environmentally induced forms (e.g., Åberg 1937), but this is really a field for experimental investigations.

The contradictory reports on regeneration indicate that we need to know more about the exact conditions for sexual and asexual reproduction, and the frequency with which such conditions occur in the field. Research on demography and population processes should be rewarding but is technically difficult. Great care must be taken to avoid marking methods that could affect survival or regeneration of the shoots. Little is known about the genetical structure of *Sphagnum* populations (Daniels 1982, 1985a, b; Cronberg 1989; McQueen 1985). How many clones are involved in a single hummock? Do genetical individuals differ in measurable physiological characteristics?

I have cited a number of investigations on the physiological ecology of *Sphagnum*. Data from such studies could be used to predict species interactions in the field, and attempts have been made by Titus and Wagner

(1984) and Hayward and Clymo (1983). However, a complete model would be complicated. Not only would one need data on the responses to temperature, light, and water content (and their interactions), but it would also be necessary to measure these variables in the field or model them from microclimatic and water-level measurements.

Caution is needed when interpreting long-term dynamics in *Sphagnum* vegetation. In ombrotrophic or near ombrotrophic habitats the plants are directly exposed to changes in the environment. High pollution levels are detrimental to all species, but lower levels might alter competitive abilities in a nonpredictable way. In Britain even small additions of N decrease the growth of *Sphagnum* (Press et al. 1986), but in a less polluted area in Ontario, additions of N led to increased growth (Bayley et al. 1987). Malmer (1990) found that although N deposition in Sweden had increased during the last decades, there were only minor changes in nitrogen concentration in the plants. He proposed that the mosses might have responded through increased growth. The effect of an increase in atmospheric CO_2 concentration and global warming on *Sphagnum* species composition is unpredictable. The temperature response of *Sphagnum* species is generally broad (Silvola 1985, Harley et al. 1989), and the plants seem to respond to increased CO_2 concentration only when they are wet (Silvola 1990). Therefore, the effect of climatic change probably depends most on changes in precipitation and humidity. All changes that affect the water table will probably also alter the relations between species. Chapman and Rose (1991) found a decrease in the frequency of several species after afforestation of surrounding areas, and the decrease was different in different species.

Sphagnum assemblages provide a reasonably simple system in which both plants and environment can be manipulated to test ecological ideas, the only drawback being the slow growth rate. There is no substitute for long-term studies. In my experiments I found that results after three to five years differed considerably from those after nine to 11 years. Research in *Sphagnum* ecology has for some time been integrated with studies in morphology, physiology, and, more recently, genetics. There is also a tradition of integrating descriptive and experimental studies in the field with studies under more controlled conditions. Such integrations are necessary to gain further understanding of the mechanisms that create the patterns we observe in the mires.

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